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MOLT AND BREEDING IN POPULATIONS OF THE SOOTY TERN *STERNA FUSCATA*

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I have recently discussed (Ashmole, 1963) the breeding cycles of the Sooty Tern *Sterna fuscata* in all parts of its range. Although there are many areas for which adequate information is lacking, it appears that this species in different localities shows three different types of breeding cycle: namely, every twelve months, every nine and one half months, and every six months. In the places where breeding occurs every six months it has not yet been shown whether the same individuals breed in successive breeding periods, but I am at present carrying out work on Christmas Island (Pacific Ocean) designed to determine this.

During study of a large number of Sooty Tern skins in United States and British museums I observed an unexpected difference in the state of the primaries between samples of birds from populations where breeding is annual and from populations where breeding occurs every six months. This difference, described in the present paper, suggests that Sooty Terns in populations where six-monthly breeding occurs have

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evolved special modifications of the species' normal molt program, which enable them to breed at approximately six-month intervals and yet to replace their remiges often enough to maintain reasonable flying efficiency.

Sooty Terns in most populations appear to have a pattern of molt similar to that in a number of other tern species: that is, they undergo a postnuptial or "basic"[1] molt after breeding in which all feathers are replaced, and a prenuptial or "alternate"[2] molt shortly before the onset of breeding which does not involve the primaries or secondaries. Although Dwight (1901) says "The Terns undergo two complete moults in a year. . .," I know of no tern species for which there is adequate evidence that all the remiges are replaced twice each year. In some species none of the remiges are replaced more than once, while in others the inner primaries are replaced twice, the outer ones only once (Ashmole, in prep.). In the Sooty Tern I have found no indication that any of the primaries are replaced more than once between one breeding period and the next.

As in other terns, molt and breeding in the Sooty Tern are more or less mutually exclusive. (However, Brown Noddies *Anous stolidus* on Ascension Island and perhaps elsewhere sometimes breed and molt at the same time (Dorward and Ashmole, 1963).) Few museum specimens are accompanied by information as to whether the individuals were involved in breeding activities when collected, but Table 1 shows that most Sooty Terns collected on breeding grounds in all parts of the world have complete sets of primaries and rectrices. From some localities there are a few birds just completing the replacement of their primaries (primary molt scores 98 and 99), while from some breeding stations there are birds which have recently started a molt (primary molt scores nearly all below 30).[3] I have already shown (Ashmole, 1963) that on Ascension Island individuals complete a molt before starting to breed, but some at least start their postnuptial molt before their chicks

[1, 2] These terms are those advocated by Humphrey and Parkes (1959).

[3] "Primary molt scores" are stages on the scale from 1 (= molt of primaries just started) to 99 (= molt of primaries almost completed); for details of the method of scoring see Ashmole (1962).

TABLE 1. Molt of primaries and rectrices of Sooty Terns collected on breeding grounds in different areas.[1]

Locality	Number of birds examined	Primaries: Proportion of birds molting	Primaries: Range in scores of molting birds[2]	Rectrices: Proportion of birds molting
GULF OF MEXICO AND W. INDIES				
Corpus Christi, Texas	17	0	—	0
Virgin Is.	12	0	—	0
EQUATORIAL ATLANTIC				
Fernando Noronha	33	.21	2-28, 98	.15
Ascension I.	107	.23	1-20	.13
SOUTH ATLANTIC				
Trinidade/Martin Vaz	11	0	—	0
INDIAN OCEAN				
Laccadive Is.	11	.18	2, 7	.09
NORTH PACIFIC				
Laysan	39	.03	98	.05
I. Isabela, Mexico	11	.18	2, 13	.09
I. Socorro	15	.20	4, 24, 48	.20
Clipperton I.	24	.04	99	.13
EQUATORIAL PACIFIC				
Christmas I.	16	.19	2, 98, 98	.06
Culpepper/Wenman, Galapagos	10	.30	All 98	.10
SOUTH PACIFIC				
Lord Howe I.	13	0	—	.23
Norfolk I.	10	.10	4	.10
Kermadec Is.	18	0	—	0
Tonga	11	0	—	0
Suvorov I.	40	.30	1-24	.15
Kauehi, Tuamotu Arch.	26	.04	98	.04
Marquesas Is.	19	.21	All 98	.05
Oeno	13	0	—	0

Notes. 1. Only breeding localities from which I have examined at least ten birds are included in this table.

2. See footnote in text for explanation of "primary molt scores."

become independent. Both on Ascension and elsewhere body molt of Sooty Terns occurs almost entirely while the birds are absent from the breeding grounds; I have so little information about it that I shall not consider it further in this paper.

PRIMARIES

Examination of molting birds on Ascension, and of skins of molting individuals, shows that in the Sooty Tern molt of the primaries normally starts with the first (innermost) feather and progresses outwards to the tenth (outermost long primary). Sooty Terns when breeding should thus have the innermost primaries oldest and the outer ones progressively newer, the whole series forming a smooth sequence. This was found to be the case in 86 per cent of all skins of birds collected on the breeding grounds and not in process of molt. However, in some birds there are striking differences in the condition of adjacent primaries; one finds a sudden break in the normal age-sequence part way through the series. This I have called a "discontinuity."[4] It should be emphasized that the discontinuities were not caused merely by molt in progress when the bird was collected; most individuals were not molting at all, and in the few which had recently started a molt the arrangement of old and new feathers at the discontinuity could not be explained as a result of the molt then in progress. It was evidently the result of an unusual molt sequence in the past, followed by a cessation of molt prior to breeding.

[4] Like many other species (Dwight, 1901) Sooty Terns have a pale "frosting" or "silvering" on the dark primaries and secondaries, which gradually wears off, thus making it easy to detect large differences in the age of adjacent feathers. I have recorded discontinuities only when the difference in the condition of adjacent feathers was sufficiently striking for there to be no doubt that they were of very different age. In badly set specimens it is difficult to assess the relative ages of the small inner primaries, especially as they tend to be protected from wear by the overlying secondaries. I may therefore have overlooked relatively new innermost primaries in some birds, and the figures for the occurrence of discontinuities between primaries 1 and 2 must be considered as minimum ones. Discontinuities further out in the series are not likely to have been overlooked, and there were few birds in which I was doubtful whether the feathers had been molted in regular sequence.

Discontinuities are found at all points in the primary series, but Table 2 (from which molting birds are excluded) shows that they are not distributed at random. Nearly all populations (see Table 3 for details) contain a small proportion of birds with first primaries much newer (occasionally much older) than the second, but in most populations (grouped in the bottom row of Table 2) discontinuities at other points in the primaries are rare. The sample from Ascension is separated since not only does it contain an especially large proportion of birds with discontinuities between primaries 1 and 2, but it also has a number with discontinuities between primaries 2 and 3;

TABLE 2. Distribution of discontinuities in the primaries of Sooty Terns collected on Ascension, on the Phoenix and Line Islands, on Bedout Island, and in the other localities mentioned in Table 3.

Locality	Number of wings examined		Number (above) and percentages (below) of wings with discontinuities at each point in the primaries $\frac{1}{2}$	$\frac{2}{3}$	$\frac{3}{4}$	$\frac{4}{5}$	$\frac{5}{6}$	$\frac{6}{7}$	$\frac{7}{8}$	$\frac{8}{9}$	$\frac{9}{10}$	No. and % of wings with no discontinuities
Ascension Island	164 (=82 birds)	No.	20	8	1	2	0	0	0	0	0	133
		%	12	5	0.6	1	0	0	0	0	0	81
Phoenix and Line Islands	64 (=32 birds)	No.	2	0	2	2	5	6	8	7	12	34
		%	3	0	3	3	8	9	13	11	19	53
Bedout Island	10 (=5 birds)	No.	2	2	0	0	0	0	0	4	2	2
Other areas	946 (=473 birds)	No.	59	7	6	5	5	4	0	3	5	854
		%	6	0.7	0.6	0.5	0.5	0.4	0	0.3	0.5	90

Notes. 1. Molting birds are not included.

2. For each locality, the upper figures are the numbers of *wings* which show discontinuities at each point in the series of primaries. Wings are used rather than birds since the two wings on a single bird sometimes have discontinuities in different places.

3. The lower figures show the number of discontinuities at each position as percentages of the number of wings examined. Since there are sometimes two discontinuities in one wing, and both are included in the figures given, the percentages total more than 100 in some cases.

these are rare in other populations. Samples from two areas only contain an appreciable number of birds with discontinuities further out in the series than the second primary. One of these areas includes the Phoenix Islands and Line Islands in the central equatorial Pacific, while the other is represented by Bedout Island off the northwest coast of Australia. The distribution of discontinuities in the wings of birds from these areas (Table 2) seems certainly to indicate that many birds in these populations have a very different molt program from the birds breeding on Ascension and in the other localities from which specimens were examined.

Table 3 shows that, from population to population, there is no correlation between the frequency of occurrence of discontinuities between primaries 1 and 2 and that of discontinuities at other points in the series. Thus while 21 out of 38 birds from the Phoenix and Line Islands have discontinuities among pri-

TABLE 3. Occurrence of discontinuities among the primaries in adult Sooty Terns from different breeding areas.

Geographical area	Occurrence of discontinuities only between primaries 1 and 2: Number of specimens available	Occurrence of discontinuities only between primaries 1 and 2: Number (and proportion) with discontinuities	Occurrence of discontinuities among primaries 2-10: Number of specimens available	Occurrence of discontinuities among primaries 2-10: Number (and proportion) with discontinuities
GULF OF MEXICO AND W. INDIES (incl. *Corpus Christi* (Texas), *Virgin Is.*)	74	13 (.18)	80	4 (.05)
EQUATORIAL ATLANTIC				
Fernando Noronha, Rocas Reef	34	2 (.06)	38	4 (.11)
Ascension I.	82	10 (.12)	106	6 (.06)
SOUTH ATLANTIC (*Trinidade/Martin Vaz*, St. Helena)	19	0 (—)	19	0 (—)
INDIAN OCEAN (incl. Gloriosa, Seychelles, Rodriguez, *Laccadive Is.*, Chagos)	21	2 (.10)	24	1 (.04)
NORTHWEST AUSTRALIA (Bedout I.)	5	1 (.20)	5	3 (.60)

TABLE 3 (Continued)

Geographical area	Occurrence of discontinuities only between primaries 1 and 2: Number of specimens available	Occurrence of discontinuities only between primaries 1 and 2: Number (and proportion) with discontinuities	Occurrence of discontinuities among primaries 2-10: Number of specimens available	Occurrence of discontinuities among primaries 2-10: Number (and proportion) with discontinuities
NORTHWEST PACIFIC .... Paracel Is., Philippines, Ryu Kyu Is., Bonin Is., Marianas)	13	3 (.23)	13	1 (.08)
NORTH CENTRAL PACIFIC .... (Wake, Hawaiian chain incl. *Laysan,* Johnston)	79	2 (.03)	82	0 (—)
NORTHEAST PACIFIC .... (Revilla Gigedo Is. incl. *Socorro, Clipperton,* Lower California, west coast of Mexico)	61	1 (.02)	63	2 (.03)
EQUATORIAL PACIFIC				
MARSHALL Is.	5	1 (.20)	5	1 (.20)
PHOENIX Is. (Howland, Baker, ... Canton, Enderbury, Phoenix)	9	1 (.11)	11	9 (.82)
LINE Is. (Palmyra, *Christmas,* .... Jarvis, Malden, Starbuck)	23	0 (—)	27	12 (.44)
GALAPAGOS Is. (*Culpepper/Wenman*)	10	1 (.10)	10	1 (.10)
SOUTHWEST PACIFIC .... (*Lord Howe, Norfolk, Kermadec Is.,* Fiji, *Tonga,* Samoa)	53	4 (.07)	55	1 (.02)
SOUTHEAST PACIFIC				
Cook Is., Society Is., Tubuai Is., .. Tuamotu Is. incl. *Kauehi, Marquesas Is., Oeno,* Henderson, Ducie, Easter, San Felix	72	3 (.04)	73	1 (.01)
Suvorov, Tongareva	34	0 (—)	42	3 (.07)

Notes. 1. Only adult birds collected on the breeding grounds or within a few miles of them are included in this table.

2. Birds which were in process of primary molt are excluded, with two exceptions: (a) birds whose tenth primaries only were growing have been included, and (b) birds whose first and/or second primaries only were growing, have been used in the right-hand section but not in the left-hand section of the table: this accounts for the differences between the columns showing "Number of specimens available" in the two sections.

3. Where ten or more birds were available for examination of primaries 2-10, from one island or from a group of islands within a circle of radius 25 miles, the name of the island or group is italicized.

maries 2 to 10, only 1 out of 32—less than the average proportion—have discontinuities between primaries 1 and 2. Only on Ascension, as already mentioned, are there an appreciable number of birds in which primary 2, together with 1, is strikingly different in age from the rest. Probably in this case birds with the first and second primaries very different in age from the next outwards should be classed with those in which only the first primary is affected.

I suspect that discontinuities far out in the series are normally produced under quite different circumstances from those between primaries 1 and 2. I have already suggested with respect to the Ascension population (Ashmole, 1963) that birds with first (or first and second) primaries newer than the next outwards may be young birds breeding for the first time; in immature Sooty Terns successive sequences of primary replacement often overlap, so that as one sequence is nearing completion with the growth of the outermost primaries, another sequence is starting with the innermost ones. If molt stops for breeding at the completion of one sequence, the outermost feathers will be new, but so may be the innermost ones, with a discontinuity outside them.

It is not possible to explain in this way the extremely high incidence of discontinuities (Table 3) among the outer primaries in the samples from the Phoenix and Line Islands, while the small sample from Bedout Island may also require a different explanation. It can be no coincidence that it is on certain of the Phoenix Islands and Line Islands, alone of the places from which I have examined an appreciable number of specimens, that Sooty Terns are known to have two breeding periods each year (Ashmole, 1963).

It has been argued (Ashmole, 1963) that the Sooty Terns on Ascension are breeding as often as they can—that breeding, followed by a complete molt, occupies about nine and a half months. But if this is the minimum time needed by the Ascension birds, it is difficult to see how the birds in the Phoenix and Line Islands (where there are two breeding periods each year) could breed and undergo a complete molt in a period of only six months. It is therefore not surprising that it has been tentatively suggested in the past (Richardson and Fisher,

1950; Hutchinson, 1950; Chapin, 1954) that in the areas where breeding occurs every six months, different populations of birds might be involved in successive breeding periods, so that each individual would breed only once a year. I also felt that this must be the explanation, until I examined specimens of the Sooty Terns from the islands concerned, and found that many of the breeding birds had some old and some new primaries, and had evidently not undergone a complete molt between breeding periods.

As it has been pointed out, Sooty Terns in other parts of their range, where breeding occurs only once each year, have a straightforward complete replacement of all their remiges after breeding. If the individuals on the Phoenix and Line Islands were also breeding only once a year, how could one explain the fact that many of them do not have a complete set of new remiges when they start breeding? The most reasonable hypothesis seems to be that at least some individuals breed in successive breeding periods and replace only some of their wing feathers in the short interval in between. It is likely, however, that no one individual breeds in every breeding period.

The sample from Bedout Island (N.W. Australia) is very small, but three out of the five birds show discontinuities among primaries 2-10. Sooty Terns have so far only been recorded as breeding in autumn on Bedout. However, it would not be surprising if they were found to have two breeding periods there each year, since Serventy (1952) has shown that they breed in autumn on islands to the north of Bedout, but in spring on islands further south (see Appendix in Ashmole, 1963, for details). Bedout is at about the latitude at which several other species of sea birds change from autumn to spring breeding, and some of them are already known to breed in both seasons, on Bedout and certain other islands (Serventy, 1952).

Of the other localities from which there are reasonably large samples, Fernando Noronha (where the interval between successive breeding periods has not yet been determined) has most birds with discontinuities among primaries 2-10, but the proportion is far lower than in the samples from the Line Islands and the Phoenix Group. Of the latter, the Line Islands have the lower proportion, but even this is significantly higher than

among the Fernando birds ($P < .01$). It is evident, therefore, that the populations from the Line and Phoenix Islands show peculiarities which are almost entirely absent in the other populations sampled. This is expected on my hypothesis that peculiarities in the molt normally occur only in individuals which breed in successive breeding periods about six months apart.

Table 3 shows that although the proportion of birds with discontinuities among primaries 2-10 is far higher in both the Phoenix and Line Islands than in any other area apart from Bedout Island, it is appreciably higher in the small sample from the Phoenix Group than in that from the Line Islands. This difference as it stands is statistically significant (at the 5 per cent level), but both samples are heterogeneous (birds collected from several different islands, in different years and at different stages in the breeding periods), so I doubt whether it is meaningful.

Examination of the precise arrangement of new and old feathers in the primaries of birds from the Phoenix and Line Islands and from Bedout Island, may help towards an understanding of the molt program in these populations and of the way in which breeding and molt are interrelated; some actual examples are therefore given below. In the examples, N represents an apparently brand new feather, (N) a newish one, (O) an oldish feather, and O an old, worn feather. Where a series of adjacent feathers have been replaced in a regular sequence, they may grade from one category to another; in such cases the two terminal members of the series are joined by an arrow headed towards the newest feather. The figures 1, 2, 3 and 4 represent successive stages in the growth of a feather (see Ashmole, 1962:255).

		1	2	3	4	5	6	7	8	9	10
1. Suvorov	L.	N	N	N	O	O	O	O	O	O	O
	R.	N	N	N	O	O	O	O	O	O	O
2. Fernando Noronha	L.	1	(N)	(N)	(N)	(N)	(N)	(N)	(N)	(N)	O
	R.	1	(N)	(N)	(N)	(N)	(N)	(N)	(N)	(N)	O
3. Jarvis I.	L.	1	(N)	(N)	(N)	(N)	O	O	O	O	O
(Line Is.)	R.	(N)	(N)	(N)	(N)	(N)	O	O	O	O	O

		1	2	3	4	5	6	7	8	9	10
4. Enderbury I. (Phoenix Is.)	L.	(N)	→	→	→	→	→	→	→	→	N
	R.	(N)	→	→	→	→	→	→	→	N	O
5. Fernando Noronha	L.	O	→	→	→	→	(O)	(N)	(N)	(N)	(N)
	R.	O	→	→	→	→	(O)	(N)	(N)	(N)	(N)
6. Baker I. (Phoenix Is.)	L.	(O)	(O)	(O)	N	N	(O)	(O)	(O)	(O)	(O)
	R.	(O)	(O)	(O)	N	N	(O)	(O)	(O)	(O)	(O)
7. Jarvis I. (Line Is.)	L.	4	1	(N)	(N)	(O)	(O)	(O)	(N)	(N)	(N)
	R.	3	(N)	(N)	(N)	(O)	(O)	(O)	(N)	(N)	(N)
8. Palmyra I. (Line Is.)	L.	N	N	N	N	N	(O)	(O)	N	N	N
	R.	N	N	N	N	N	N	N	N	N	N
9. Christmas I. (Line Is.)	L.	(O)	→	→	(N)	O	O	O	O	(N)	(N)
	R.	(O)	→	→	(N)	O	O	O	O	(N)	O
10. Enderbury I. (Phoenix Is.)	L.	(N)	→	→	→	N	(O)	(O)	(O)	N	(O)
	R.	(N)	→	→	→	N	(O)	(O)	(O)	N	(O)

In most birds with discontinuities among primaries 2-10, both from areas where breeding occurs annually and from those where it occurs every six months, the feathers inside the discontinuity are newer than those outside it (see examples 1-4). This condition is the one which would arise if a normal sequence of primary replacement stopped part way through the series. Patterns of the type shown in example 5, in which there is a definite discontinuity between old feathers on the inside and newer ones on the outside, would result if, after primary replacement had stopped part way through the series for breeding, it later started again where it had left off, and then continued outwards.[5] However, the condition shown in example 5 is uncommon in all Sooty Tern populations. This suggests that normally, when a bird with the inner feathers newest (as in example 1) starts to molt again, the innermost primaries, rather than those immediately outside the discontinuity, are replaced first; this is in fact what is occurring in examples 2 and 3.

[5] Something equivalent to this certainly occurred in the replacement of the secondaries of some Black Noddies *Anous tenuirostris* on Ascension Island (Ashmole, 1962).

The other examples shown are of the more complex situation in which there is more than one discontinuity among the primaries in one or both wings. Patterns of this type, which are found in a significant proportion of the birds from areas where breeding occurs every six months, have not yet been found among birds from annual-breeding populations. They could not be produced during a molt program in which each primary was always replaced in regular sequence outwards through the series, but they could arise if an incomplete primary replacement was succeeded, after the breeding period, by another incomplete molt, and if feathers replaced late in the first of these molts tended to be skipped during the next. In this case the bird in example 1, if it underwent another incomplete molt, might in the next breeding period be in a condition similar to example 6, for instance:

	1	2	3	4	5	6	7	8	9	10
L.	(O)	(O)	(O)	N	N	N	N	O	O	O
R.	(O)	(O)	(O)	N	N	N	N	O	O	O

Another partial molt could lead to conditions comparable to those in examples 7-10, for instance:

L.	N	N	N	(O)	(O)	(O)	(O)	N	N	N
R.	N	N	N	(O)	(O)	(O)	(O)	N	N	N

or

L.	N	N	N	(O)	(O)	(O)	(O)	N	N	O
R.	N	N	N	(O)	(O)	(O)	(O)	N	N	O

It will be clear from what has been said that it is not necessary to postulate a random molt sequence to account for the complex patterns of old and new primaries found in the wings of some Sooty Terns. The indications are that in these birds as in all other terns molt in the primaries proceeds from the inside outwards, but that many individuals in populations where breeding occurs every six months fail to replace all their primaries between successive breeding periods, and that subsequent molts are modified by the presence in their wings of a mixture of old and new feathers.

SECONDARIES

As in other tern species, replacement of the secondaries in Sooty Terns starts much later than that of the primaries, but is completed at the same time or only a little later. Replacement normally starts at the two ends of the series of secondaries, and it is some of the middle feathers (often numbers 12 and 13 counting from the carpal joint inwards) which are the last to be replaced. After the complete replacement of the secondaries in this manner there should be no appreciable discontinuities within the series, but the feathers at the two ends of the series will be oldest, and the middle ones newest. This is in fact the situation found in nearly all specimens from most Sooty Tern breeding colonies, including Ascension Island (Table 4). This must imply that all the secondaries are replaced once between breeding periods. However, in several populations

TABLE 4. Numbers of Sooty Terns with discontinuities among the secondaries, in relation to the incidence of discontinuities among primaries 2-10, in different populations.

Geographical area	Birds without discontinuities among primaries 2-10: Number examined	Birds without discontinuities among primaries 2-10: Number with discontinuities among secondaries	Birds with discontinuities among primaries 2-10: Number examined	Birds with discontinuities among primaries 2-10: Number with discontinuities among secondaries
Gulf of Mexico and W. Indies	72	0 (+2?)	2	1
Ascension I.	74	1	6	1
Indian Ocean	22	0 (+1?)	1	1
Phoenix Is.	2	2	8	6 (+2?)
Line Is.	13	4 (+1?)	11	11
South Pacific (incl. Marquesas, but not Suvorov)	116	4 (+1?)	1	0
Suvorov	26	9 (+6?)	3	2 (+1?)

Notes. 1. Birds undergoing molt of primaries or secondaries are excluded, except for those in which only the first primaries have so far been shed.

2. Additional figures in brackets, followed by question-marks, represent birds whose secondaries show probable, but not striking, discontinuities.

birds are found which have some secondaries much older than the rest. I did not examine the secondaries of all specimens, and there were a good many doubtful cases, so I cannot give reliable figures for the frequency of this peculiarity in all populations. However, Table 4 gives the information for those populations from which the secondaries of a fair proportion of the available specimens were examined.

As might be expected, the populations in which many birds show discontinuities in the primaries (Phoenix and Line Islands) also contain many birds with discontinuities among the secondaries. However, in these populations some of the birds without discontinuities in the primaries, nevertheless have secondaries which do not seem to have been replaced in a smooth sequence: evidently the molt cycle is not entirely normal even in these birds.

Among localities where discontinuities in the primaries are rare, the island of Suvorov, south of the equator in the central Pacific, is the only one from which I have a fairly large sample, in which many birds have discontinuities among the secondaries (Table 4). In these birds some of the middle secondaries tend to be much older than the rest, suggesting that the secondary molt has stopped before completion. This situation invites comparison with the Black Noddies on Ascension Island (Ashmole, 1962), where the primary molt was apparently never cut short at the start of breeding, but some of the old middle secondaries, which are normally molted slightly later than the last primaries, were sometimes retained through the breeding period and replaced immediately after it. The occurrence of a similar phenomenon among the Sooty Terns on Suvorov suggests that the breeding cycle there may be abnormal in some respect, but there is very little information on the times of breeding (Ashmole, 1963).

RECTRICES

Replacement of the tail feathers of Sooty Terns normally starts with the outermost feathers (number 6 on each side), the central pair (number 1) being molted next; molt probably then continues in the sequence 2, 3, 5 and 4. It is possible that

in the annual-breeding populations all the rectrices are then replaced again before the next breeding season, but in the Ascension population there was evidence that the outer pair alone are replaced twice (Ashmole, 1963). In the Ascension birds the outer webs of the outermost feathers are normally white in the breeding period, but are more often, if not always, dark in the non-breeding period. In other populations there is much variation in the color of these feathers, and samples from different populations sometimes also differ markedly. In some areas nearly all the birds taken on the breeding grounds have entirely white outer webs to the outer rectrices (69 out of 82 birds from the North Central Pacific), but in other places (e.g. Fernando Noronha, the Southeast Pacific, the Phoenix and Line Islands, and Suvorov) the proportion is much lower. It is likely that in the populations in which breeding occurs every six months not even the outermost rectrices are always replaced twice between successive breeding periods. I cannot suggest any explanation of the different frequencies with which dark color is present in the outer webs of these feathers in other populations.

DISCUSSION

The data presented in this paper, together with the information on the times of breeding of various Sooty Tern populations given by Ashmole (1963), show that the schedule of breeding and molt evolved among the Sooty Terns of the Phoenix and Line Islands is remarkable both in that breeding occurs every six months, and in that the program of molt is flexible to a unique degree. It appears that an individual sometimes undergoes a complete molt without interruption but at other times replaces only some of its primaries and secondaries between one breeding cycle and the next.

I have already mentioned that in the populations where breeding occurs every six months, individuals which have undergone only a partial molt before breeding generally have the outer primaries older than the inner ones. Since the outer primaries are also more subject to wear, it is not surprising to find some individuals with outer primaries in extremely poor

condition while breeding. These birds are doubtless below their maximum flying efficiency, but if the curtailed molt has enabled them to breed in a breeding period which they would otherwise miss, the disadvantage may on balance be outweighed. However, it is clear that the molt program in the Phoenix and Line Island populations, in which the inner primaries are on an average replaced more often than the outer ones, although the latter get more wear, is not the most efficient that might be evolved. More birds would be close to maximum flying efficiency for more of the time if molt always started from where it had left off, so that the primaries were always replaced in order of age. This evidently happens sometimes but cannot be common.

Although I have argued that the presence of discontinuities among the primaries of breeding individuals from the Phoenix and Line Islands implies that these birds were involved also in the previous breeding period only six months before, I am not suggesting that individuals breed *every* six months. It seems unlikely that a pair could raise a chick successfully in one breeding period and yet be ready to breed again in the next breeding period only six months later. With the time required for courtship plus incubation for a month and feeding the young for two to three months (longer if the juveniles are not independent as soon as they leave the colony), very little time would be left before the next breeding period. I would guess that birds which raise a chick in one breeding period may then undergo a complete molt, missing the next breeding period; this would account for the proportion of birds from the Phoenix and Line Islands which appear to have undergone a perfectly normal and complete molt. Many of the birds, however, losing their eggs or their chicks while fairly young, could be ready to try again in the next breeding period, after only a partial molt.

This reasoning is of course highly speculative, and further discussion of the factors controlling the schedule of breeding and molt in the Sooty Terns of the Phoenix and Line Islands will be profitable only when we have more information on the sequence of events in individual birds from one of these populations.

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This account of molt in populations of *Sterna fuscata* forms a complement to my study of the species on Ascension Island during the course of the British Ornithologists' Union Centenary Expedition (Ashmole, 1963). The present paper is a product of my examination of a large number of skins of *Sterna fuscata* during the summer of 1960, while I was the holder of a Seessel fellowship at Yale University. I am most grateful to Professor G. E. Hutchinson who suggested a study of specimens of the species and who with Dr. S. Dillon Ripley enabled me to visit Yale. I must also thank Dr. Philip S. Humphrey, who gave me much of his time during my work in the Yale Peabody Museum, and whose wide knowledge of molt was a constant stimulant. My visit to Yale was made while I was a member of the Edward Grey Institute of Field Ornithology, Oxford; it is a pleasure to thank the Director, Dr. David Lack, for encouraging me to go to Yale, for helpful discussion of my work and for reading a draft of this paper. My wife has also made many helpful criticisms of the manuscript.

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seum of Natural History, the Chicago Natural History Museum, the United States National Museum and the Bernice P. Bishop Museum, Hawaii.

SUMMARY

The Sooty Tern *Sterna fuscata* in most parts of its range breeds at the same season in each year, and study of museum specimens shows that the individuals replace all their remiges and rectrices between breeding seasons. On Ascension Island, where breeding occurs every nine and one half months, there is also a complete molt between successive breeding periods. However, among birds from the Phoenix Islands and Line Islands in the central equatorial Pacific, where breeding occurs every six months, many individuals have "discontinuities" among the primaries and secondaries, indicating that they have not undergone a complete molt between successive breeding periods. These populations have apparently evolved a uniquely flexible molt program, such that under certain circumstances (perhaps the successful rearing of a chick) breeding is followed by a complete molt, but often molt stops and the bird breeds again before all of the primaries and secondaries have been replaced. It is suggested that because of this flexibility in the molt, individuals are sometimes able to take part in successive breeding periods only six months apart.

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